

SENSORY RESPONSES OF NEMATODES^{1/}

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INTRODUCTION:--Nematodes respond to changing environmental factors including chemicals, mechanical stimuli, light, temperature, and perhaps gravity and electric currents (Croll, 1971). This sensitivity may enable nematodes to locate favorable niches and react toward suitable feeding sites and mates. Mechanisms of sensory responses have been inferred from studies of behavior, limited physiology, and particularly morphology, but more complete understanding is needed if applications are to be made toward improved nematode control.

CHEMORECEPTION:--The liquid environment of nematodes includes gradients of chemicals. These chemicals may act as stimuli and thereby attract or repel nematodes to or from the source of the stimulant. For example, plant roots, which are potential food for many nematodes, create gradients through liberation and utilization of chemicals. Furthermore, metabolic activities of microorganisms at the root's surface result in similar gradients. Abundant research supports the attractiveness of various chemical gradients to nematodes, and Klingler (1965) regards CO₂ and certain amino acids as most important. However, some nematodes have narrow host ranges, and one might suspect that more specific (chemical ?) stimuli may be involved, that enable the parasite to "recognize" and respond to a particular host.

Sexual reproduction is necessary to the survival of many nematode populations, but potential mates may be too widely dispersed to depend on chance encounters. Green (1967) demonstrated that exudates from some species of *Heterodera* females were attractive to males. More recently, Bone and Shorey (1977) disrupted the capacity of males of *Nippostrongylus brasiliensis* Travassos to locate females, by regulating gradients of chemical sex attractants.

There is substantial behavioral evidence that nematodes respond to chemicals, but little is known about sites or mechanisms of detection. Chemoreceptive neurons (nerve cells) are stimulated only by direct contact with molecules; therefore, receptive endings of these neurons must penetrate the nematode cuticle, without compromising the support and protection provided by the exoskeleton. Nematode organs for chemical detection might be expected to include one or more neurons which terminate in a cavity or channel which is open to the exterior.

Many investigators have suggested that amphids, present in the head region of nematodes, are chemoreceptive, and electron microscopy confirms that amphidial neurons occur in open channels. Ward *et al* (1975) found that defective amphidial nerves are present in nonchemoreceptive mutant nematodes, substantiating that amphids are chemoreceptive. Papillae, small raised areas which might appear to be mechanoreceptive in the light microscope, occur in many regions of the nematode, but are particularly common anteriorly. Baldwin and Hirschmann (1975) demonstrated that certain papillae have very minute openings and therefore, are likely to be chemoreceptive. In the posterior region of the nematode, phasmids have been thought to be chemoreceptive, but recently Clark and Shepherd (1977) have shown that spicules (male copulatory organs) may also be able to detect chemicals.

MECHANORECEPTION:--Chemoreception aids nematodes in locating a host or mate; whereas mechanoreception may elicit finer responses such as host penetration, feeding, or positioning for copulation. Mechanical stimuli might be direct (tactile) or conducted a distance from the source (viz. turbulence, vibration), and can be transferred through the cuticle. Therefore, nerves of mechanoreceptors are not necessarily directly exposed to the environment, although Clark and Shepherd (1977) have noted that exposed neurons might be both mechanoreceptive and chemoreceptive. The simplest mechanoreceptors are free nerve endings underlying unmodified cuticle, and function, for example, to detect direction of strain on the body wall. Many mechanoreceptors include modifications of cuticle, such as papillae, warts, setae, and bristles. Papillae that are interpreted as mechanoreceptive have no openings to the exterior. The pressure stimulus is transferred through a thin layer of cuticle to an underlying chamber of dense material (liquid ?) which contacts sensory neurons. Elongate mechanoreceptors include setae and bristles which, when disturbed, stimulate nerve receptors at the base. Crofton (1968) has suggested that the lateral placement of amphids suggests a capacity to detect movement or turbulence, in addition to chemicals. Although nematode mechanoreceptors are diverse, specific capabilities of individual receptors are only inferred from position and morphology. Ward *et al* (1975) propose that the role of individual mechanoreceptors might be determined by examining nematode mutants with defective mechanical sensitivity, for fine-structural aberrations of suspected receptors.

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OTHER SENSITIVITIES:--Nematodes respond to some stimuli for which the cuticle would present little barrier, and thus, receptors for such stimuli are not characterized by cuticular modifications. Many nematodes respond to temperature gradients; for example, El-Sherif and Mai (1968) showed that the heat gradient produced by the metabolism of a plant, might be sufficient to attract some species, but temperature-sensitive neurons have not been identified. Similarly, some nematodes seem to respond to electric currents and gravity, but corresponding receptors are not known. Investigators have suggested that nematodes respond to some stimuli through general effects on metabolism or the neuromuscular system. However, it is also possible that receptors exist which are not sufficiently distinct to have been morphologically identified. Some nematodes respond to light. Certain soil species are repelled by sunlight; this response might preempt their attraction to associated solar heat, so that they avoid lethal ultraviolet rays or desiccation. On the other hand, certain parasitic species might be attracted to light, which would be an advantage if exposure at the soil surface increases contact with potential hosts. Freshwater and marine nematodes, attracted to light, might be led to areas of algal growth for feeding. Light sensitivity appears to be of 2 forms in nematodes: 1) "dermal light sensitivity" in which a specific receptor is not apparent; 2) specialized light reception dependent on sensitive pigments or ocelli. Although the dermal light sense is apparently most common, many marine and some freshwater nematodes have pigment spots, which, in association with a "lens", are called ocelli. Such pigment spots may be photosensitive, or, as Burr and Burr (1975) suggest, the pigment may act to shade a separate photoreceptor, providing sensitivity to light direction.

CONCLUSION:--Understanding of nematode sensory systems has recently progressed, particularly with respect to fine structure of receptors. Microchemical procedures, including characterization and isolation of attractants, will further expand this knowledge. These investigations will not only be valuable to fundamental sensory physiology and systematics, but more importantly, as Bone and Shorey (1977) have noted, may give man the ability "to manipulate the chemical signals to his advantage and to the disadvantage of the nematodes". Such control would be environmentally safe and would not tend to exert selection pressures which favor pesticide-resistant pathogens.

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